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Surround modulation in visual cortex can predict border-ownership selectivity: psychophysical study of border-ownership-dependent tilt aftereffect

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Recent physiological studies revealed that neurons in the macaque visual cortex encode the direction of a figure along a contour (border ownership, BO). Although their cortical mechanisms have not been clarified, a computational model for BO has suggested that surround modulation in early vision can play an important role. Here we examined psychophysically how the strength of BO-dependent tilt aftereffect (BO-TAE) is modulated by a stimulus outside the adapted location in relation to the strength of surround modulation reported in physiological experiments. The results showed systematic change of the strength of BO-TAE, depending on the difference in orientation and spatial frequency between the bars placed outside and at the adapted location, indicating a crucial role of surround modulation in the neural mechanism underlying BO selectivity.

OCIS codes: 330.3790, 330.5020, 330.5510, 330.7310, 330.7320.

1. INTRODUCTION

To recognize objects, the visual system must separate them from the background. Information projected onto the retina undergoes extensive analysis in the cerebral cortex. The first stages in this process take place in the primary and secondary visual areas V1 and V2 (e.g., [1]). Neurons in these areas process fundamental characteristics of visual images, such as orientation and color of line segments, with the analysis being limited for each neuron to a relatively small region of the input scene that is called a classical receptive field (CRF). Because the size of the CRF is a few degrees or less at the eccentricity of 5° [2], these neurons would seem only to extract local information on shapes of objects or scenes. If this is indeed the case, the functional role of early vision would be merely to provide local information to higher visual cortices.

In contrast to this view of the functional role of early visual cortices in the scene analysis, a number of physiological studies have suggested that neurons in V1 and V2 are critically involved with a global shape analysis that extends beyond the reach of the individual neuron's CRF [3,4]. In recent neurophysiological studies of the macaque visual cortex, some neurons showed differential responses to a contour placed within the CRF, depending on the direction of a figure that "owns" the contour (Fig. 1) [5,6]. This suggested that global image analysis occurs in an early stage of visual information processing that takes into account border ownership (BO). However, it remained unclear how the BO information is computed at the cellular level.

Another line of neurophysiological studies in early visual areas showed that responses of neurons to a stimulus contained within their CRFs can be modulated (suppressed or enhanced) by another stimulus presented simultaneously outside the CRFs [7–9]. Consider, for instance, the study of macaque V1 neurons by Jones *et al.* [10], which used drifting gratings as stimuli. While stimulating the CRF of a neuron by a grating of optimal orientation, the experimenters varied the orientation of another grating outside the CRF. They observed that the response of the neuron depended on the orientation difference between the two gratings. This response modulation could be in the form of either enhancement or suppression. Maximum suppression was achieved when the two orientations were the same (iso-orientation suppression), and maximum facilitation was achieved when the two orientations were orthogonal (cross-orientation facilitation). While these experiments were neither aimed specifically at investigating the possible neuronal circuitry for BO nor performed in V2/V4 where more BO-selective neurons were found than in V1, their results may help to explain how BO selectivity can be formed by the neurons' receptive field structure. Indeed, a computational model based on the notion of surround modulation [11] showed

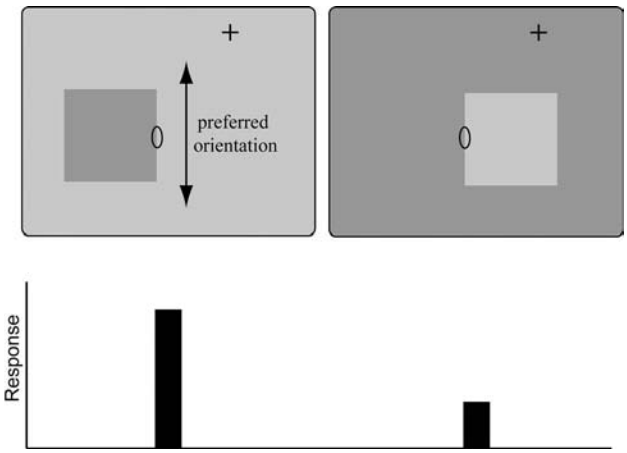

Fig. 1. Schematic illustration for border-ownership (BO) selectivity. In this illustration a square shape is presented on either the left or right side of the neuron's classical receptive field (CRF) against a uniform background, while a vertical edge is aligned to its preferred orientation. Although a local contrast polarity within the CRF is identical in both stimulus conditions, this neuron strongly responds to the stimulus in which a square is shown on the left side of the CRF, as represented by the height of the black bars. This characteristic was termed as "border ownership," found in the macaque visual cortex [5]. Note that the "+" symbol and the ellipse indicate a fixation point and the outline of the CRF, respectively.

high consistency and robustness in signaling BO for various stimuli in a manner compatible with the physiological behavior of the neurons reported by Zhou *et al.* [5].

A recent human psychophysical study demonstrated that BO dependent tilt aftereffect (BO-TAE; [12]) can be induced even when the stimulus contours lack smooth continuity [13]. BO-TAE is a variant of tilt aftereffect in which the aftereffect occurs only when adaptation and test stimuli are presented on the same side of the border. Interestingly, the configuration that maximizes the suppressive effect of the surround modulation reported in primate V1 cells [10] induced significant BO-TAE [13]. This motivated us to undertake further psychophysical study of the contribution of surround modulation to the organization of BO.

In the present paper, we examined how the configuration of two vertical lines in the stimulus changes the strength of the BO-TAE in relation to the strength of the surround modulation expected from the physiological experiments [10]. In the BO-TAE experiment, subjects were first shown trapezoid stimuli presented alternatively on the right or left side of the fixation point so that a given retinal location was adapted by oblique edges of the trapezoid stimuli, which were mirror symmetric with respect to a vertical line passing through the fixation point. After the adaptation, two bars were shown as the test stimulus, and subjects were asked to judge the side to which the bar presented at the adapted location appeared tilted. The test stimuli were also alternatively shown on the right or left side of the fixation point. We specifically looked at how the strength of the observed BO-TAE was affected by the spatial relationship between the bar in the adaptation stimulus shown at the intended adaptation location and the bar in the test stimulus distal to the adapted location. The results showed the dependence of BO-TAE on the orientation of the distal bar: BO-TAE is maximized when the orientation of an adaptation bar matches that of a distal test bar and is gradually weakened as the difference in the orientation of the two bars increases. This phenomenon is consistent with the response modulation of our model evoked by the orientation dependence on surround modulation.

2. METHODS

We hypothesized that surround modulation is the key to forming BO selectivity. To understand how BO selectivity is formed at the cellular level, we measured the strength of BO-TAE while systematically changing the spatial relationship of the proximal bar in the adaptation stimulus and the distal bar in the test stimulus, so that the strength of the surround effect driven by the distal bar in the test stimulus would change accordingly. Specifically, we manipulated the orientation of the distal bar in the test stimulus while keeping constant the orientation of the proximal bar in the adaptation stimulus whose location was switched so that the BO is altered. Thus, the angular difference of the two bars between the adaptation and the test stimuli was altered (Experiment 1 and Experiment 2). In addition, we also increased the width of either the proximal bar or the distal bar in the test stimulus (Experiment 3).

We examined how these manipulations of the test stimulus affected the strength of BO-TAE using a procedure similar to the one employed in our previous report [13]. BO-TAE is a variant of tilt aftereffect in which a line is perceived tilted after adaptation. The uniqueness of BO-TAE lies on the fact that the aftereffect occurs only when the adaptation stimulus and the test stimulus are presented on the same side relative to the adapted location. First, subjects were adapted to a trapezoid formed by four line segments with a width of 2 mm (0.14 arc deg), as shown in the left panel of Fig. 2 (adaptation phase). The trapezoid was not filled. The size of the trapezoid was 89 mm (6.3 arc deg) in height and 73 mm (5.2 arc deg) and 96 mm (6.8 arc deg) in top and bottom width, respectively. The edge of a trapezoid near the fixation point was tilted −15° (clockwise) when the trapezoid was shown on the right and +15° (counterclockwise) when it was shown on the left. The midpoint of the slant edge of the trapezoid was positioned on the left side of the fixation point by 0.86 arc deg from the fixation point (adapted location). The trapezoids were shown alternatively to the right or left side by flipping the trapezoid horizontally over the adapted location. Therefore, the midpoint of the slant edge was always at the adapted location, but the direction of the slant was alternated in accordance with the position of the trapezoid. The trapezoid was shown for 500 ms with an interval of 100 ms on each side. In total, subjects were adapted to 80 pairs of the trapezoid, resulting in a total adaptation time of 96 s. Following the adaptation phase, the test phase consisted of presentating a pair of test stimuli (test phase; Fig. 2, right), followed by four pairs of trapezoids as additional adaptation during the test phase (in-test adaptation, not shown in the figure). Each test stimulus was presented for 200 ms, with an interval of 1000 ms. The vertical bar at the adapted location

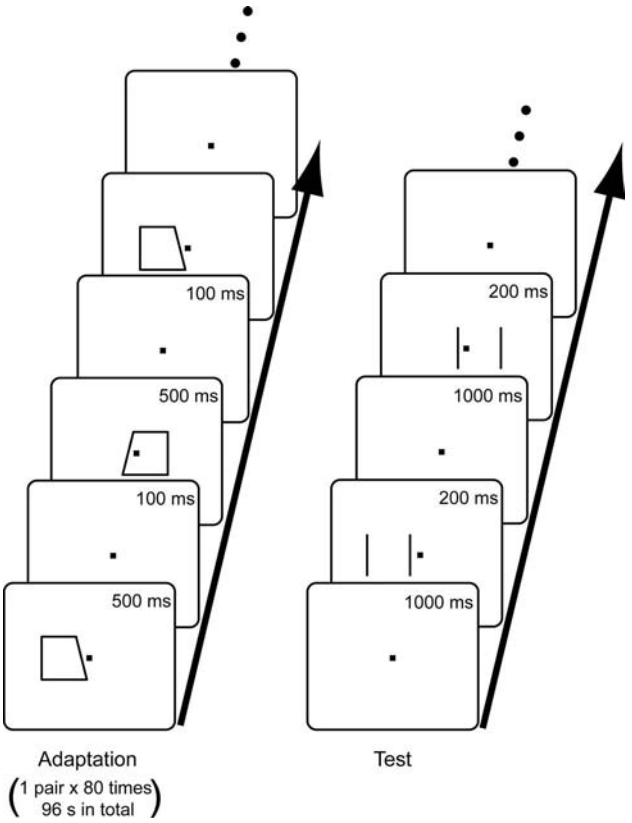

Fig. 2. Experimental procedure. (Left) Stimulus configuration during the adaptation phase. Midpoint of the tilted edge (15°) of a trapezoid was situated at 0.86 arc deg beside a fixation point (indicated by a small black dot). Two trapezoids were shown alternatively for 500 ms each with a 100 ms blank period, and 80 pairs were presented. This gives a 96 s adaptation in total. (Right) Paradigm of stimulus configuration during the test phase. A test stimulus was shown on the left or right side of the adapted location for 200 ms each. As an example of the test stimuli, the two vertical bar stimulus is shown here. The range of orientation of the vertical bar at the adapted location varied randomly within ±2° at intervals of 0.2°. Subjects were asked to report to which side the vertical bar of the square at the adapted location appeared tilted. In the test phase, adaptation with four pairs of trapezoids followed the two test stimuli.

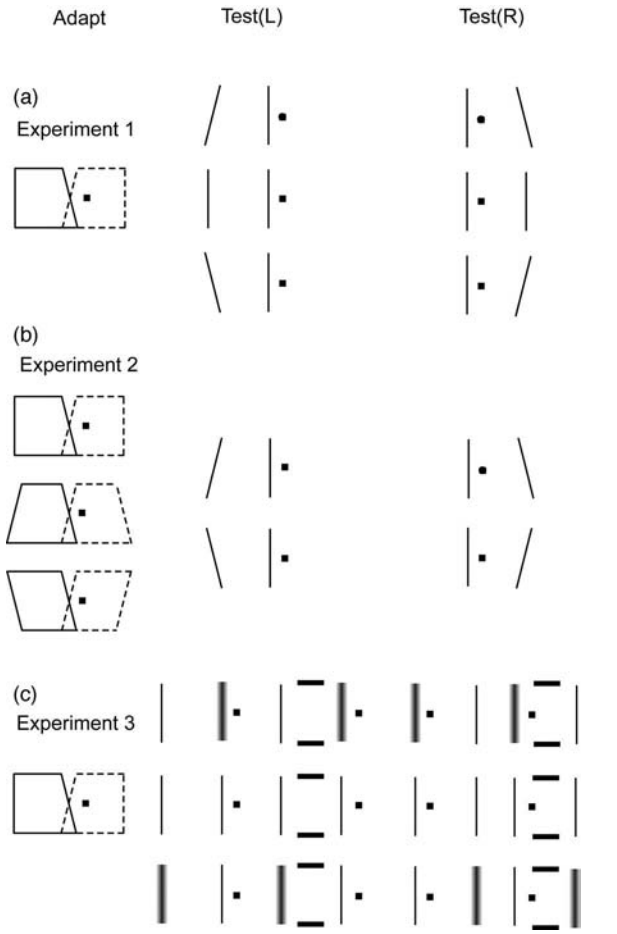

Fig. 3. Adaptation stimulus and test stimulus. In all the experiments, subjects were first exposed to an adaptation stimulus (left column). In Experiments 1 and 3, the adaptation stimulus was a trapezoid. In Experiment 2, an isosceles trapezoid and a parallelogram were added in addition to a trapezoid. Solid and dotted lines indicate the stimulus shown on the left and right side of the fixation point (a small black dot), respectively. The center and right columns show the test stimuli presented on the left and right side of the fixation point, respectively.

(test bar) was rotated randomly at each presentation (constant stimuli method). The orientation ranged between −2.0° and +2.0° at intervals of 0.2°. This procedure resulted in the presentation of 21 pairs of the test stimulus. The in-test adaptation comprised four pairs of the trapezoids, shown under identical conditions to the first adaptation phase. In each condition, the subjects were asked to judge the side to which the bar presented at the adapted location appeared tilted (two-alternative forced choice). The entire procedure (adaptation phase and test phase) was repeated five times.

According to the aim of each experiment, the shapes of the adaptation and test stimuli were manipulated (Fig. 3). In Experiment 1, a pair of vertical bars was shown as a test stimulus. The bar distal to the fixation point was rotated by −15°, 0°, and +15°, while the shape of the adaptation stimulus was a trapezoid [Fig. 3(a)] to see the effect of a distal bar on the amount of BO-TAE. In Experiment 2, we added two variants of the adaptation stimulus (an isosceles trapezoid and a parallelogram) to examine how combinations of adaptation stimuli and test stimuli affect the strength of BO-TAE [Fig. 3(b)]. In Experiment 3, the same trapezoid presented in Experiment 1 was used as an adaptation stimulus, but we changed the width of one of the two vertical bars of the test stimuli [Fig. 3(c)] to determine whether a spatial frequency of the stimulus given at the adapted location needs to be matched between the adaptation and the test stimuli to induce BO-TAE and also to see whether changes of the spatial frequency of the stimulus at the distal location affects the strength of BO-TAE. We used six test stimuli in Experiment 3, half of which had two horizontal bars. One of the two vertical bars was thin or thick; the horizontal bars were of intermediate width. The width of the thickest vertical bar was ten times as large as that of the thinnest one. The width of the horizontal bars was half that of the thickest vertical bar. The luminance of the thickest vertical bar was modulated by a Gaussian function. Specifically, the luminance of 1 pixel at the center of 61 pixels was the same as the luminance of the stimuli used in Experiments 1 and 2. The luminance was gradually reduced

from the center to the edge of the bar on both sides by a Gaussian function. The position at the tenth pixel from the center corresponded to one standard deviation. The width of the thinnest vertical bars was same as that used for the adaptation and test stimuli in Experiments 1 and 2, but the luminance was changed in the same way that the luminance of the thickest vertical bars was controlled. The length of the vertical bar of the test stimuli in all three experiments, including the rotated bars distal to the fixation, was 71 mm on the computer display, corresponding to 5.0 arc deg. The distance between the midpoints of the vertical bars was also 71 mm. The length of the horizontal bars in Experiment 3 was 70% of the length of the vertical bars.

Stimuli were presented on a 21" (1 in.=2.54 cm) CRT monitor (DELL Inc., Texas, USA) with a spatial resolution of 1600×1200 at a refresh rate of 75 Hz. The monitor was located in a dark room with a dim light. Subjects viewed the monitor from a distance of 80 cm with their head on a chin rest. All subjects had normal or corrected-to-normal vision. Stimuli were white with a brightness of 40.1 cd/m^2.

Psychometric functions were fitted by logistic regression analysis to the plots of the response ratio to the counterclockwise perception of the vertical bar of the test stimulus at a given θ ($-2.0 \leqslant \theta \leqslant 2.0$). BO-TAE was defined as the difference between the 50% threshold of the psychometric functions for each side on which the test stimulus was presented: $\theta_{estimate}^{left} - \theta_{estimate}^{right}$. Note that a *positive* value of the 50% threshold ($\theta_{estimate}$) indicates that subjects tended to perceive the vertical bar as tilted *clockwise* as a result of adaptation; i.e., the vertical bar must have been tilted physically farther counterclockwise to induce the perception of vertical. Data analysis was performed using R (freeware under the GNU's General Public License) and S-PLUS (Insightful Corp., Washington, USA).

3. RESULTS

We hypothesized that BO selectivity involves the surround modulation mechanisms that were identified by physiological means in visually responsive neurons and therefore that the BO-TAE would also change its strength when the effectiveness of the surround modulation is altered. In Experiments 1 and 2, we examined whether the strength of BO-TAE changes according to the change in the strength of the surround modulation expected from the orientation difference between the bars in the center and the surround of the adapted location. In Experiment 3, we investigated whether the dependence of BO-TAE on the spatial frequency of the stimulus is consistent with that of the surround modulation.

A. Experiment 1

We investigated the dependence of BO-TAE on the orientation of a distal bar in test stimuli that fall onto the surrounding region. Specifically, we examined whether the strength of BO-TAE is modulated by the difference in orientation between the proximal bar in adaptation stimuli (adaptation bar) and the distal bar in test stimuli (distal test bar). To investigate the orientation dependence of BO-TAE, we employed three types of test stimuli with the distal bar rotated +15°, 0°, and −15°, as illustrated in Fig. 3(a). We employed these angles because the iso-orientation suppression has relatively sharp tuning [10] and because larger angles tend not to evoke BO-TAE due to the corruption of figural shape [13].

Figure 4 shows the observed BO-TAE for the three subjects as a function of the orientation difference between the adaptation bar and the distal test bar. Error bars indicate 95% confidence intervals computed by the bootstrap method [13]. BO-TAE was statistically significant when the orientation difference between the adaptation bar and the distal test bar was 0° and 15° but was not significant for 30°. A one-way analysis of variance (one-way ANOVA; factor, the orientation of the distal bar at −15°, 0°, and 15°) revealed a significant effect of the orientation of the distal test bar on the strength of the observed BO-TAE ($p < 0.01$).

The result suggests that the more cross oriented the distal test bar and the adaptation bar become, the weaker the observed BO-TAE is. Here we describe how this result can be explained by our model of BO selectivity [11,14]. In our model, BO-selective neurons have asymmetric distribution of the excitatory and inhibitory regions outside the CRFs, as reported in the physiological studies of the early visual cortices [10,15]. This receptive field structure determines the preferred side of a figure; when a facilitatory region of a cell is overlaid with part of a visual stimulus whose contour is stimulating the cell's CRF, it enhances the cell's responses, and therefore the cell behaves as if the contour is *owned* by the side where the facilitatory region is present.

Suppose there are three groups of such neurons whose preferred orientation differ [cells A, B, and C in Fig. 5(a)]. Here it is assumed that these neurons have their CRFs at the adapted location. The neurons whose preferred orientation match the orientation of the adaptation bar (cell A) will be activated most strongly; therefore they will be

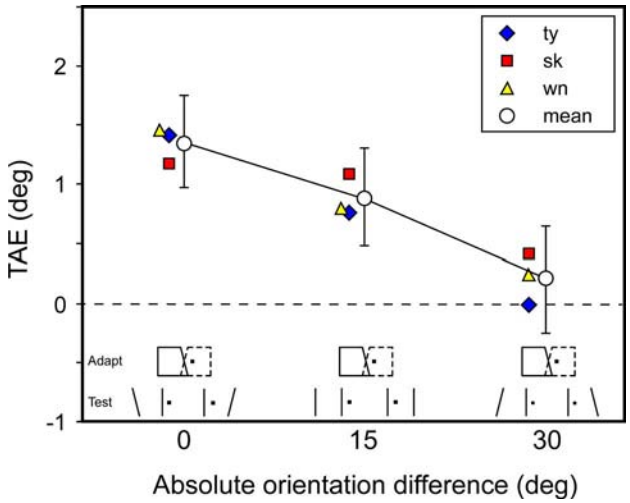

Fig. 4. (Color online) Observed BO-TAE as a function of the absolute orientation difference in Experiment 1. Three types of filled icons identify the subjects, and the open circles show the mean BO-TAE among the three subjects, with the error bars indicating 95% confidence intervals. BO-TAE was estimated by the bootstrap method described in the text. The larger TAE is observed for the more similar orientations between the distal test bar and the adaptation bar.

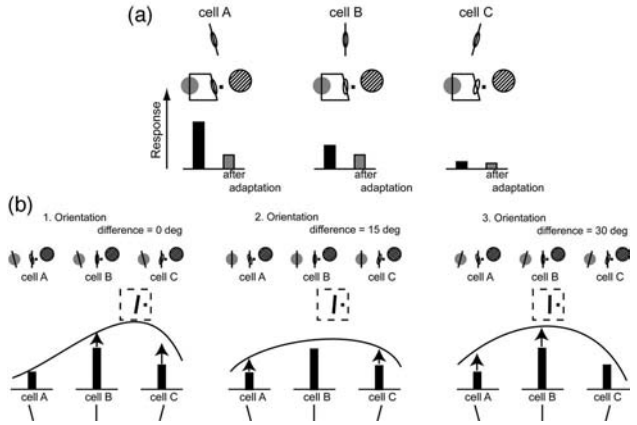

Fig. 5. Model of BO-TAE. We consider three groups of BO-selective neurons whose optimal orientation is different (cell A, cell B, and cell C). (a) Edge of a trapezoid stimulates the cell's CRF (indicated by an ellipse). Here we assume, for convenience and simplicity, that BO-selective cells have an excitatory region on the left side of the CRF (a gray circle) and an inhibitory region on the right side of the CRF (a hatched circle). The optimal orientation of cell A matches the orientation of the edge of a trapezoid. Thus, responses of cell A are strongest among the three cells (a black bar). In turn, the responses of cell A would be most effectively fatigued after adaptation (a gray bar). (b) After adaptation, the distal test bar stimulates the excitatory region, which induces cross-orientation facilitation on the responses of the cells (an arrow). The effectiveness of the facilitation depends on the difference between the orientation of the distal test bar and the optimum orientation. When a population of BO-selective cells is considered by the sum of the responses (all three black bars with arrows), the position of the peak of the population response determines how the test bar is perceived (indicated by the bar inside the dashed square with a fixation spot).

most effectively fatigued. The neurons whose orientation does not match the orientation of the adaptation bar will also be fatigued, but in a less effective manner, as the difference between the preferred orientation and the orientation of the adaptation bar becomes larger.

In the three different test stimuli, the bar within the CRFs was consistently vertical, which is assumed to be the preferred orientation of cell B. The orientation difference between the test bar and the preferred orientation of cell A and cell C was exactly the same (15° in absolute value). Therefore, the expected order of the response strength to the test bar alone after adaptation would be cell B > cell C > cell A [see black bars in Fig. 5(b)], and this order would be same for the three test stimuli [Fig. 5(b) and 1–3]. We assume that the strength and the direction of BO-TAE are determined essentially by the position of the peak of the responses along the orientation axis after the responses of these neurons are summed. This is compatible with an explanation for the conventional tilt aftereffect [16–18]. Therefore, the strength of BO-TAE would be equal in the three test conditions [Fig. 5(b) and 1–3] if BO-TAE could be explained completely by adaptation alone.

However, taking into account surround modulation, the difference in the strength of BO-TAE among the three test conditions in the experiment can be well explained. In the present model the distal test bar is placed in the excitatory region outside the CRF. Though cross-orientation facilitation was examined while the CRF was stimulated by the optimal orientation of the neurons, the orientation tuning of the neurons that exhibited effects of cross-orientation facilitation was not always very sharp [10]. Thus the proximal test bar whose orientation differed from the neurons' preferred orientation by 15° would not abolish the effect of cross-orientation facilitation. Under this condition, when the orientation difference between the adaptation bar and the distal test bar is zero [Fig. 5(b) and 1], the response of cell C would increase relative to the expected response to the test bar alone [black bar with arrow in Fig. 5(b) and 1], because the preferred orientation of cell C and the distal test bar are cross oriented and thus facilitated. However, such facilitation would not occur or would be very weak in the response of cell A, because the preferred orientation of cell A and the orientation of the distal test bar are parallel (i.e., iso-oriented). This results in the peak of the population response shifting toward the preferred orientation of cell C; thus the test bar is perceived tilted to the right. Similarly, when the absolute orientation difference between the adaptation bar and the distal test bar is 30° [Fig. 5(b) and 3], the response of cell A would be further facilitated, but the response of cell C would not. Then the shift of the peak response would be small—even smaller than the shift expected when the absolute orientation difference between two bars is 15° [Fig. 5(b) and 2], where enhancement of the response could occur in both cell A and cell C. Note that when the orientation difference is 30°, the test bar was not perceived to be very clearly tilted toward the preferred orientation of cell A (i.e., counterclockwise), presumably because the total responses of cell A [black bar with arrow in Fig. 5(b) and 3] would not be strong enough to shift the peak responses toward the preferred orientation of cell A.

B. Experiment 2

In Experiment 1, we found that the deviation of the orientation between the adaptation bar and the distal test bar is one of the factors that modulated the strength of BO-TAE, and we argued that this result can be explained by the surround modulation. The surround modulation must have been also present in the adaptation phase, and different adaptation stimuli would activate the same group of BO-selective neurons to different extents. If the relationship between the adaptation bar and the distal test bar is the most critical factor that influences the strength of BO-TAE, the orientation dependence of

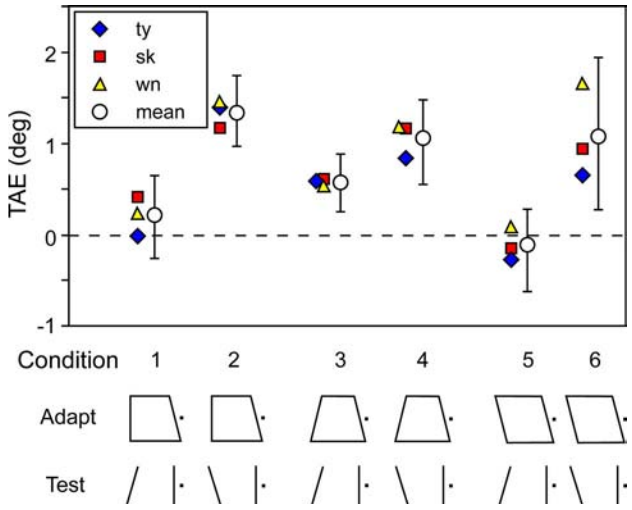

Fig. 6. (Color online) Observed BO-TAE in Experiment 2. There were six different combinations of the adaptation stimuli and the test stimuli. The observed BO-TAE is plotted by conditions. The notation is the same as in Fig. 4. In most of the cases, a significant TAE is observed if the adaptation bar and the distal test bar have the same orientation.

BO-TAE found in Experiment 1 would be still present even when we employ different shapes of adaptation stimuli in which the orientation of the distal adaptation bar is changed.

In this experiment, we examine whether the dependence of BO-TAE on the orientation difference between the adaptation bar and the distal test bar can be obtained with variants of the adaptation stimulus. The shapes of the adaptation stimuli consisted of a standard trapezoid used in Experiment 1, an isosceles trapezoid, and a parallelogram. The test stimuli and the experimental paradigm were the same as in Experiment 1, except that one test stimulus composed of a pair of two vertical bars was excluded.

Figure 6 shows the observed BO-TAE from three subjects as a function of the combination of the adaptation and the test stimuli. BO-TAE was statistically significant when the orientation of the distal bar in the test stimuli is −15° (the bar tilted counterclockwise) for all adaptation conditions but is not significant for two out of three adaptation conditions when the orientation was +15°. A two-way ANOVA was performed on the type of the test stimuli (−15° or 15°) × the type of the adaptation stimuli (the same trapezoid as in Experiment 1, the isosceles trapezoid, or the parallelogram). A significant main effect was found in the type of the test stimuli ($p=0.012$). The type of the adaptation stimuli did not reach significance ($p=0.12$), and there was no significant interaction ($p=0.07$). Thus, the orientation of the distal test bar affected the amount of BO-TAE, reproducing the result of Experiment 1 with variants of adaptation stimuli. Although the amount of BO-TAE is slightly smaller for the adaptation with the parallelogram compared to the isosceles trapezoid, the difference was not statistically significant.

C. Experiment 3

Blakemore and Campbell [19] reported that TAE depends on the spatial frequency; TAE is evoked only when the width of a line segment shown during the test phase is the same as that shown during adaptation. Because both TAE and BO-TAE are assumed to involve orientation-selective neurons, it is possible that BO-TAE would depend on spatial frequency, that is, would require that the width of the adaptation bar and the test bar be the same. In addition, a recent physiological study has shown that surround modulation can be observed with a stimulus that combines the preferred spatial frequency for the CRF and a lower frequency for outside the CRF [20]. Because our model of BO-selective neurons relies on surround modulation, it predicts that a significant BO-TAE will be observed even when the width of the distal test bar is larger than that of the proximal test bar. Although increasing the width of the bar does not correspond precisely to lowering the spatial frequency of grating stimuli, it is reasonable to assume that neurons that respond to a lower frequency grating would also respond to a wider bar stimulus.

The test stimulus was a pair of two vertical bars; the width of either bar could be changed compared to the width of the adaptation stimulus. We predicted that when a proximal bar of a test stimulus is widened with respect to that of the adaptation stimuli, BO-TAE would not be observed because of the spatial frequency characteristics of TAE mentioned earlier. However, the contribution of the widened distal test bar would be quite similar to that of the original bar; therefore, the strength of the BO-TAE induced in both stimulus conditions would be comparable.

Figure 7 shows the observed BO-TAE from the three subjects. In experimental conditions 1 and 4 (see Fig. 7), the lower boundary of the bootstrap-estimated 95% confidence interval was negative (−0.00017 and −0.081, respectively), indicating that the observed BO-TAE with the wider test bar was not significantly greater than 0 at the $p=0.025$ level. To further assess the significance of the BO-TAE in these two conditions, we calculated the proportion of the bootstrapped values that exceeded zero. In condition 1, the proportion was 0.965, and in condition 4 it was 0.929. This indicates that the induced BO-TAE was

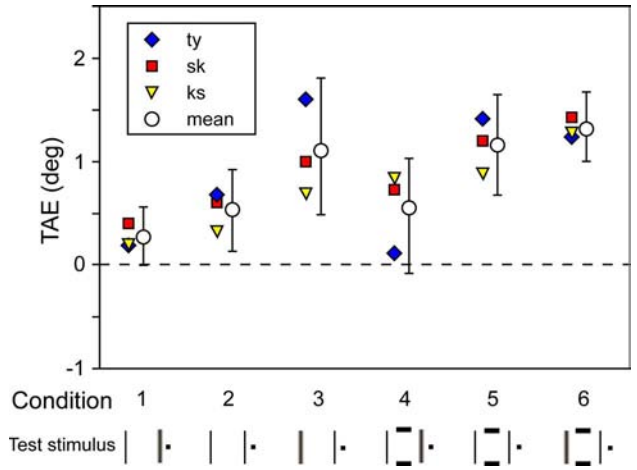

Fig. 7. (Color online) Observed BO-TAE in Experiment 3. There were six different test stimuli, and the observed BO-TAE is plotted by conditions. The notation is the same as in Fig. 4. A significant TAE is observed even if the distal test bar is thicker that the adaptation bar.

significantly larger than zero in condition 1 ($p=0.035$) but not in condition 4 ($p=0.071$). To test whether BO-TAE depends on the bar width, we performed a two-way repeated-measures ANOVA on the width of the bars (proximal wider, same, or distal wider) × the presence of the horizontal bars (presence or absence). A significant main effect was observed in the width of the bars ($p=0.038$). The effect of the presence of horizontal bars did not reach significance ($p=0.12$), and there was no significant interaction ($p=0.36$). Because we were particularly interested in whether the widened distal bar affected the magnitude of the observed BO-TAE, we ran a two-way repeated-measures ANOVA again with the data for conditions 2 and 5 (thin bars; the same width as the adaptation stimulus) and 3 and 6 (wider distal test bars), excluding conditions 1 and 4 (wider proximal test bars). There was a significant main effect of the width of bars ($p=0.0046$). The main effect of the presence of the horizontal bars and the interaction of the two factors did not reach significance ($p=0.072$ and $p=0.37$, respectively). As seen in Fig. 7, the BO-TAE induced by the test stimuli with wider distal test bars was stronger, but the difference in the strength of the BO-TAE between conditions 5 and 6 was very small.

To examine whether the wider distal test bar induced stronger BO-TAE, we calculated the difference of the mean BO-TAE between conditions 2 and 3 (no horizontal bars) and between conditions 5 and 6 (with horizontal bars) and calculated the probability of obtaining the observed amount of the difference. First, we pooled the bootstrap-estimated BO-TAE for each subject in the two conditions and randomly assigned each estimate to either of the two conditions. The number of the estimate was exactly the same as the original number. This randomization was performed for all three subjects; we calculated the mean BO-TAE over three subjects in each condition and iterated 4999 times. By adding the original observation of the difference of the mean BO-TAE between the two conditions, 5000 new estimates of the difference in the mean BO-TAE were obtained. We considered the original difference in the mean BO-TAE between the two conditions to be significant if the probability of obtaining a difference in the mean BO-TAE greater than or equal to the original difference was smaller than 0.05. As a result, the difference of the mean BO-TAE in the two different pairs of the conditions was far greater than the estimated values after randomization, and thus the difference was significant ($p=0.0002$).

There are two major findings in this experiment. First, the observed BO-TAE was weaker, or even statistically insignificant, in one of the two tested conditions when the test bar was wider than the adaptation bar. This indicates that BO-TAE shares similar characteristics with the conventional TAE in the sense that both depend on the spatial frequency of the stimuli, suggesting a possibility that common neuronal mechanisms might be involved in the two TAEs. Second, a significant BO-TAE was observed for the thick distal bar (i.e., conditions 3 and 6) while the widths of the test bar and the adaptation bar were kept same. Additional statistical tests showed that the induced BO-TAE was even stronger with the thick distal bar in the test. These results are consistent with our prediction based on the physiological findings that the surrounding modulation is effective even if there is difference in the spatial frequency between inside and outside the CRF [20]. Tables 1–3 summarize the observed BO-TAE in the three experiments.

4. DISCUSSION

We conducted a series of psychophysical experiments in which BO-TAE was studied in relation to the surround modulation of the neurons in the early visual cortex, which we assume to be involved in BO selectivity. In Experiments 1 and 2 we found that the absolute orientation difference between the adaptation bar and the distal test bar significantly changed the strength of BO-TAE; the shape of the adaptation stimulus was less important. In Experiment 3 we demonstrated that BO-TAE depends on the spatial frequency in the sense that the adaptation bar and the proximal test bar must have the same width. In addition, we showed that the distal test bar does not necessarily have to have the same width as the adaptation bar to induce a significant BO-TAE. Assuming that BO-TAE involves surround modulation, the finding that the change of the width of the distal test bar does not abolish BO-TAE is consistent with our prediction based on physiological findings [20].

Although the effect of the orientation difference between the adaptation bar and the distal test bar was limited, we found that when the orientation of the two bars matched, the observed BO-TAE was maximized (Experiments 1 and 2). A model for BO selectivity proposed by Nishimura and Sakai [11,14] can explain this phenomenon as described in Subsection 3.A. The result can be explained essentially by the shape of the tuning curve of the population response of BO-selective neurons. Specifically, the difference in responses between neurons whose preferred orientation matches the orientation of the adaptation bar [see cell A in Fig. 5(b)] and neurons whose preferred orientation is most different from the adapted orientation [see cell C in Fig. 5(b)] is critical. The response of the former group of neurons is weaker than that of the latter group because of adaptation. As a result, the larger the response difference becomes, the more the orientation at the peak of the population response would be shifted to the orientation opposite that of the adaptation bar [Fig. 5(b)]. A key role of surround modulation in this model is to change the response difference by the facilitation effect. Therefore, it is important to quantify the strength of the responses of BO-selective neurons to the test stimuli before and after adaptation by physiological experiments in the future. None of the test stimuli had better continuity in shape compared to other stimuli;

Table 1. Observed BO-TAE and 95% Confidence Interval: Experiment 1

Absolute Orientation Difference (deg)	Mean (deg)	95% Confidence Interval (deg)
0	1.34	0.96–1.74
15	0.87	0.48–1.31
30	0.21	−0.26–0.65

Table 2. Observed BO-TAE and 95% Confidence Interval: Experiment 2

Condition	Mean (deg)	95% Confidence Interval (deg)
1	0.21	−0.26–0.65
2	1.34	0.97–1.75
3	0.57	0.25–0.89
4	1.06	0.56–1.47
5	−0.11	−0.63–0.28
6	1.07	0.27–1.93

therefore, the difference in the effectiveness of the three test stimuli were due to the differences in the orientation of the distal test bar, which makes different contributions to the amount of enhancement of the responses.

BO-TAE in the present study could be induced without any effect of adaptation provided that the enhancement of responses by surround modulation was effective and significantly strong. The sufficient shift of the peak responses of a population of BO-selective neurons, which is considered to be the origin of BO-TAE, could be simply the result of a contextual effect. To exclude this possibility, we conducted an additional experiment that was identical to Experiment 1 except for the absence of the adaptation phase, including in-test adaptation. Thus, in this additional experiment, the subjects were asked to report whether the proximal test bar was tilted clockwise or counterclockwise while the orientation of the distal bar of the test stimuli was varied (+15°, 0°, and −15°). The result showed that there was no BO-TAE in all three conditions. Note that we call it BO-TAE even though no adaptation is involved, because the definition for the calculation is identical. The observed BO-TAE averaged over three subjects in the three conditions (+15°, 0°, and −15°) were 0.16°, 0.20°, and 0.40°, respectively. We calculated the lower bound of the bootstrap-estimated confidence interval to see whether the mean BO-TAE was significantly larger than 0 at the 95% confidence level. In all the conditions, the lower bounds were less than 0 (−0.36, −0.23, and −0.56 for +15°, 0°, and −15°, respectively), indicating that BO-TAEs in the three conditions were not significantly larger than 0. In addition, unlike the finding in Experiment 1, there was no effect of the orientation of the distal test bar on the amount of the BO-TAE (one-way ANOVA; $p = 0.26$). Therefore, we conclude that BO-TAE in the present study is not an apparent tilt induced by surround modulation. Instead, this experiment confirmed that BO-TAE requires fatigue of a population of neurons that are BO selective.

Table 3. Observed BO-TAE and 95% Confidence Interval: Experiment 3

Condition	Mean (deg)	95% Confidence Interval (deg)
1	0.27	−0.0017–0.56
2	0.54	0.14–0.92
3	1.10	0.49–1.81
4	0.56	−0.081–1.04
5	1.13	0.60–1.66
6	1.32	1.00–1.68

In Experiment 2, we did not find a significant effect of the shapes of the adaptation stimuli on the BO-TAE. This result alone cannot rule out the presence of surround modulation for BO-selective neurons; there is a possibility that the strength of the surround modulation induced by the different shapes of the adaptation stimuli was actually different, but it did not reach significance. While there is a huge variation in the depth of the adaptation effects among different cells [21], physiological evidence [22–26] suggests that reduction of neural response after adaptation is maximized when the adapter is the most preferred stimulus for the cell along multiple dimensions, such as orientation, contrast, and direction.

In Experiment 3, we found that the widened distal test bar induced stronger BO-TAE. In the physiological experiment conducted by Webb *et al.* [20], where surround modulation was observed while a combination of the preferred spatial frequency of the grating for the CRF and a lower frequency for outside the CRF was presented as a stimulus, the orientation of the grating could be independently changed for the center and the surrounding regions. Thus, the surround effect was measured while the annulus stimulus entirely covered the region outside the CRFs within a range of 6° to 8° from the center. If this stimulus configuration is applied to our model of the structure of a receptive field for BO selectivity, where an excitatory region and an inhibitory region are asymmetrically distributed around the CRF, the modulation effect would include both iso-orientation suppression and cross-orientation facilitation, explaining the observed stronger effect. Moreover, the facilitatory effect, if even present, was not analyzed in the experiment of Webb *et al.* [20]. Therefore, a small grating stimulating only an excitatory region may show a stronger facilitatory effect when a grating with a frequency lower than that inside the CRF is utilized. If this is the case, the present psychophysical result can be explained by this physiological mechanism.

For the mechanism introduced here, if the net gain of the responses by facilitatory surround modulation depends on the magnitude of responses (i.e., the stronger the responses become, the more net gain of the responses is given), which we assume to be plausible, the difference in responses in two opponent groups of BO-selective cells (cell A and cell C in Fig. 8) becomes larger. As a result of a larger difference of responses induced by more effective stimuli, the peak of population responses of BO-selective cells will be shifted a little farther away from the adapted orientation. It is also of interest that Tsuji and Sakai [27] reported that in their simulation study, where the neural network was constructed to have BO selectivity based on surround modulation [11,14], the output of the network predicted that when the orientation of the adaptation bar and the distal test bar matched, the observed BO-TAE was maximized.

To summarize, we reported a psychophysical study of the dependency of BO-TAE on the orientation and the spatial frequency of visual stimuli, under the hypothesis that surround modulation is involved in BO selectivity. We demonstrated that BO-TAE was modulated by the orientation difference between the bar on the adapted location in the adapter and the bar distal to the adapted location in the test stimulus. We also showed that the bars

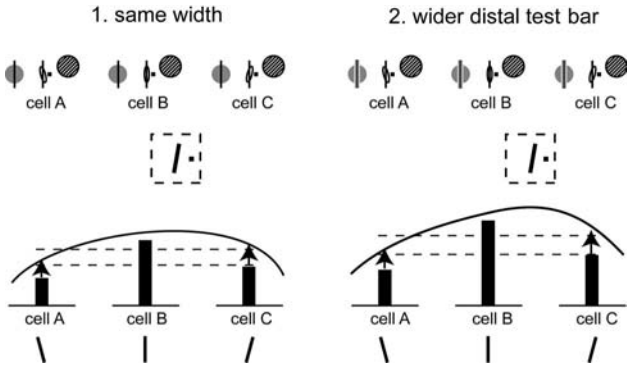

Fig. 8. Schematic illustration for a possible explanation of the result in Experiment 3. The notation is the same as in Fig. 5. As the response difference between cell A and cell C becomes larger, the observed BO-TAE also becomes larger. The response difference is represented as the distance between the two dashed lines in case 1 (same width) and case 2 (wider distal test bar). Under the assumption that the stronger the responses become, the more net gain of the responses is given, the difference in responses between cell A and cell C becomes larger in case 2 above. As a consequence of the larger difference in case 2, the peak of population responses of BO-selective cells will be shifted a little farther away from the adapted orientation, resulting in stronger BO-TAE in case 2.

placed at the adapted location must have the same spatial frequency between the adaptation phase and the test phase for BO-TAE to be induced. The bar distal to the adapted location in the test stimuli may have a lower spatial frequency to induce BO-TAE, and it induced stronger BO-TAE in the experiment. The present psychophysical results are well explained by appealing to the effects of surround modulation in the early visual cortex, suggesting that the surround effects play a crucial role in determining the BO of a contour in visual images.

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REFERENCES

1. D. J. Felleman and D. C. Van Essen, "Distributed hierarchial processing in primate cerebral cortex," Cereb. Cortex **1**, 1–47 (1991).
2. R. Gattass, C. G. Gross, and J. H. Sandell, "Visual topography of V2 in the macaque," J. Comp. Neurol. **201**, 519–539 (1981).
3. G. Baumgartner, R. von der Heydt, and E. Peterhans, "Anomalous contours: A tool in studying the neurophysiology of vision," Exp. Brain Res. **Suppl. 9**, 413–419 (1984).
4. R. von der Heydt, E. Peterhans, and G. Baumgartner, "Illusory contours and cortical neuron responses," Science **224**, 1260–1262 (1984).
5. H. Zhou, H. S. Friedman, and R. von der Heydt, "Coding of border ownership in monkey visual cortex," J. Neurosci. **20**, 6594–6611 (2000).
6. F. Qiu, T. Sugihara, and R. von der Heydt, "Figure-ground mechanisms provide structure for selective attention," Nat. Neurosci. **10**, 1492–1499 (2007).
7. V. A. Lamme, "The neurophysiology of figure-ground segregation in primary visual cortex," J. Neurosci. **15**, 1605–1615 (1995).
8. A. M. Sillito, K. L. Grieve, H. E. Jones, J. Cudeiro, and J. Davis, "Visual cortical mechanisms detecting focal orientation discontinuities," Nature **378**, 492–496 (1995).
9. K. Zipser, A. F. Lamme, and P. H. Schiller, "Contextual modulation in primary visual cortex," J. Neurosci. **16**, 7376–7389 (1996).
10. H. E. Jones, W. Wang, and A. M. Sillito, "Spatial organization and magnitude of orientation contrast interactions in primate V1," J. Neurophysiol. **88**, 2796–2808 (2002).
11. K. Sakai and H. Nishimura, "Surrounding suppression and facilitation in the determination of border ownership," J. Cogn Neurosci. **18**, 562–579 (2006).
12. R. von der Heydt, T. Macuda, and F. T. Qiu, "Border-ownership-dependent tilt aftereffect," J. Opt. Soc. Am. A **22**, 2222–2229 (2005).
13. T. Sugihara, Y. Tsuji, and K. Sakai, "Border-ownership-dependent tilt aftereffect in incomplete figures," J. Opt. Soc. Am. A **24**, 18–24 (2007).
14. H. Nishimura and K. Sakai, "Determination of border-ownership based on the surround context of contrast," Neurocomputing **58–60**, 843–848 (2004).
15. M. Ito and H. Komatsu, "Representation of angles embedded within contour stimuli in area V2 of macaque monkeys," J. Neurosci. **24**, 3313–3324 (2004).
16. C. W. Clifford, P. Wenderoth, and B. Spehar, "A functional angle on some after-effects in cortical vision," Proc. R. Soc. London, Ser. B **267**, 1705–1710 (2000).
17. M. Coltheart, "Visual feature-analyzers and the after effects of tilt and curvature," Psychol. Rev. **78**, 114–121 (1971).
18. M. J. Wainwright, "Visual adaptation as optimal information transmission," Vision Res. **39**, 3960–3974 (1999).
19. C. Blakemore and F. W. Campbell, "On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images," J. Physiol. (London) **203**, 237–260 (1969).
20. B. S. Webb, N. T. Dhruv, S. G. Solomon, C. Tailby, and P. Lennie, "Early and late mechanisms of surround suppression in striate cortex of macaque," J. Neurosci. **25**, 11666–11675 (2005).
21. D. G. Albrecht, S. B. Farrar, and D. B. Hamilton, "Spatial contrast adaptation characteristics of neurones recorded in the cat's visual cortex," J. Physiol. (London) **347**, 713–739 (1984).
22. V. Dragoi, J. Sharma, and M. Sur, "Adaptation-induced plasticity of orientation tuning in adult visual cortex," Neuron **28**, 287–298 (2000).
23. D. Giaschi, R. Douglas, S. Marlin, and M. Cynader, "The time course of direction-selective adaptation in simple and complex cells in cat striate cortex," J. Neurophysiol. **70**, 2024–2034 (1993).
24. S. G. Marlin, S. J. Hasan, and M. S. Cynader, "Direction-selective adaptation in simple and complex cells in cat striate cortex," J. Neurophysiol. **59**, 1314–1330 (1988).
25. J. R. Müller, A. B. Metha, J. Krauskopf, and P. Lennie, "Rapid adaptation in visual cortex to the structure of images," Science **285**, 1405–1408 (1999).
26. R. G. Vautin and M. A. Berkley, "Responses of single cells in cat visual cortex to prolonged stimulus movement: Neural correlates of visual aftereffects," J. Neurophysiol. **40**, 1051–1065 (1977).
27. Y. Tsuji and K. Sakai, "Orientation dependency in border-ownership dependent tilt aftereffect," J. Vis. Soc. Jpn. Suppl. **18**, 143 (2006).